I. SUMMARY

The linked questions of what is a community and how does it change through space and time are some of the most long-lasting and vexing issues in ecology. In part, this reflects the different scales of time and space from which researchers draw their data, yet the issue is of great practical importance because it impinges on decision making in conservation biology.

In offering the potential for linking differently scaled studies from both ecology and palaeoecology, ancient lakes are ideal areas in which to investigate this problem. High degrees of endemism and morphological specializations in the faunas of these lakes suggest that ecological interactions among such organisms are also likely to be complex, highly deterministic and stable, as a result of long periods of coevolved interactions. Data from long-term studies of fish ecology in Lake Tanganyika support this notion of highly evolved interactions and community stability, and have served as a general model for understanding ecological interactions in ancient lakes.

However, the highly endemic and diverse ostracods of Lake Tanganyika do not conform to this model. Ostracod species associations are extremely variable in space, probably as a result of local colonization and extinction events within local population patches. Whereas individual species show
affinities for particular environments, the assemblage observed in a given locality is highly unpredictable. Palaeoecological analyses of sediment cores also show species composition to have varied greatly over periods of hundreds of years. In some cases, however, this assemblage variability is accompanied by stability in total species richness.

These results suggest that several models of community assembly may be relevant to ancient lake faunas, and that caution must be exercised in applying any particular model of community structure or stability to conservation biology and biodiversity management.

II. INTRODUCTION

For most of the twentieth century ecologists have asked the question “What are communities?” (e.g. Clements, 1916; Gleason, 1926). Are they the result of extensive coevolution of organisms that have cohabited specific regions or environments on the earth’s surface over geologically long time intervals, or are they the chance byproducts of the association of species with similar habitat requirements? Is “diversity structure” (i.e. the component contributions of local $\alpha$ diversity, across-gradient $\beta$ diversity and regional $\gamma$ diversity; Whittaker, 1977) highly variable over time, or is the contribution of each component to total diversity within an ecosystem relatively constant? If the latter, what allows for such homeostasis? How important are factors such as predation, competitive interactions or mutualisms in structuring species associations, and are they major forces in driving evolutionary diversification? Are there emergent properties of communities at progressively larger spatial and temporal scales, and to what extent is the perception of “community” influenced by the spatial and temporal scale of sampling and data collection (Haury et al., 1978; Levin, 1992)? These questions are important not only to theoreticians, but also for conservation biologists and resource managers. In this chapter these questions will be examined from the perspective of ancient lakes, their ecosystems and their conservation biology. Reference will be made to the cichlid fishes, and especially to the ostracod crustaceans, of Lake Tanganyika, two groups for which relevant data are available.

As humans manipulate nature, either for intended purposes or incidentally through our own population growth, we have generally ignored Aldo Leopold’s well-known dictum of “intelligent tinkering”, that we keep all of nature’s interactions intact until we understand fully the potential consequences of doing otherwise (Leopold, 1953; Samways, 1996). It is central to the effort of avoiding “unintelligent tinkering”, that we understand the relative importance of particular species interactions in these lakes and what the ecosystem-level consequences are of disrupting such species-level interactions.

The theoretical and practical importance of understanding community composition and interactions has led to a variety of approaches to address this
question, foremost among which have been ecological, palaeoecological and phylogenetic perspectives. Ecologists have used simulation models, and field and laboratory monitoring and manipulation. Notable within the latter category are long-term ecological research sites (LTER sites), which can provide extraordinarily detailed records of communities and the interactions of organisms. However, even the longest running of these sites have only been monitored for about 100 years and most have been studied for only a few decades or less. So, despite the wealth of information that can be obtained about the structure and composition of these extant species assemblages, from a practical standpoint it may never be possible to uncover the origins and evolution of species associations using this approach.

Palaeoecologists have utilized the fossil record to attempt to reconstruct time-series data on species associations (e.g. Davis, 1986; Valentine and Jablonski, 1993; Brett and Baird, 1995; Pandolfi, 1996). Palaeoecological data have the advantage of covering evolutionarily meaningful time periods, through which the historical background and stability of associations can become evident. However, the temporal resolution of palaeoecological data is frequently poor and often uncertain, and the nature of interactions between species usually can only be inferred.

Phylogenetic reconstructions have the power to illustrate the sequential divergence patterns of species with known modern associations, and can reveal patterns of cospeciation through the demonstrating of matching phylogenies in closely linked groups of species (e.g. Armbruster, 1992; Moran and Baumann, 1994). However, the temporal and spatial resolution of these historical inferences is highly variable, and the results are dependent on the quality of the phylogenetic inference used.

When studying the history and durability of species interactions it is desirable to link the complementary strengths of these differently scaled approaches. Yet this is easier said than done, since not all of these types of data are available for every ecosystem. However, ancient lakes are one setting for which such complementary data are available. Furthermore, many ancient lakes have complex ecosystems with numerous endemic species, and consequently with great potential for phylogenetic reconstructions. In addition, all of these lakes are, or could be, fruitful LTER sites. More importantly, these lakes are self-contained tectonic, depositional and evolutionary systems. Their ages are often known with some certainty and highly resolved records of their long histories are preserved in their sediments.

### III. LAKE TANGANYIKA

#### A. Ecological Interactions

Lake Tanganyika is one such ancient lake, and provides an outstanding setting
for drawing links across these scales and understanding the history of species associations. This lake is one of the largest (c. 34 000 km²) and oldest freshwater lakes in the world (c. 9-12 My; Cohen et al., 1993a). For over 100 years its peculiar, endemic fauna has been a source of interest among naturalists (Smith, 1881; Moore, 1903; Fryer, this volume). Over 1500 species of protists, plants and animals have been described from the lake, perhaps 600 of which are endemic to it, and new species are being described each year (Coulter, 1991, 1994; De Vos and Snoeks, 1994; Martens, 1994; Michel 1994, this volume). Numerous studies document Lake Tanganyika’s extraordinary community complexity and species interactions on a local scale (e.g. for fish communities: Yamaoka, 1983; Takamura, 1984; Hori, 1987; Kuwamura, 1987, 1992; Hori et al., 1993) and the implications of these diverse biotic interactions for the evolution of species and communities (Fryer and Iles, 1972; Hecky and Fee, 1981; Hecky and Kling, 1981; West et al., 1991; Rossiter, 1995). Biodiversity is high in Lake Tanganyika at all levels: within habitats, between habitats and between provinces (Coulter, 1991). On a local scale species diversity is also strongly and inversely correlated with sedimentation disturbance, caused primarily by watershed erosion and sediment discharge following deforestation (Alin et al., 1999). This inverse correlation is mostly evident in the northern lake basin, where human population density is high and land use has historically been very intense (Cohen et al., 1993b).

Not only are Lake Tanganyika species diverse, but they are also highly disparate from their sister taxa outside the lake basin, both morphologically and genetically (e.g. Michel et al., 1992; Sturmbauer and Meyer, 1993; West and Cohen, 1996). The extraordinary variability seen in feeding structures, defensive mechanisms and courtship behaviours within many of the faunal groups has been used as evidence for the existence of strong (and often obligate) species interactions within Tanganyikan species assemblages. Hori et al. (1993) attribute resource partitioning among Tanganyikan cichlids to a combination of competitive displacement between feeding guilds for food resources, and commensal and mutual relationships involving various species during foraging. West and Cohen (1994, 1996) have argued that the extraordinary shell sculpturing and thickening observed in endemic Tanganyikan gastropods is probably driven by strong predation pressure from potamonautaid crabs (which have also undergone a species radiation in the lake of taxa with unusually large, shell-crushing chelae).

Collectively, this body of work supports the notion that a strong relationship exists between the extraordinary diversity of Lake Tanganyika and the complexity of what appear to be highly deterministic ecological interactions. In this view, Lake Tanganyika species flocks qualify as true adaptive radiations (sensu Simpson, 1949), in which extreme niche specialization and finely tuned adaptation to local environments or resources explain how so many species can be packed into one locality (e.g. Fryer and Iles, 1972; Liem, 1978). Some studies suggest that community integration is very tight in Lake Tanganyika,
particularly within littoral, rocky-bottom communities of cichlid fishes (Nakai et al., 1994). At one well-studied site (Mbamba, Democratic Republic of Congo), these workers have documented a relatively stable fish fauna over a time scale of 5–10 years.

B. Ostracod Ecology

The ostracods are another group of Tanganyika fauna whose ecology and evolution have been well studied, but unlike the cichlid fishes, they do not appear to conform to the pattern of community integration described above. The Tanganyikan ostracods are highly diverse: as many as 200 species may exist in the lake, almost all of which are endemic (Martens, 1994). The ostracod “radiation” actually incorporates numerous independent, monophyletic lineages (Martens, 1994; Park and Downing, this volume). Many species are highly derived (numerous endemic genera are recognized), some of which possess the hallmark “thalassoid” features of heavy calcification and spinosity and shell sculpturing well known among the Tanganyikan prosobranch gastropods (West and Michel, this volume). Phylogenetic reconstructions for one clade, the genus Gomphocycythea, suggest that speciation within at least some endemic Tanganyika lineages has been slow, and that independent lineages of Gomphocycythea have been accumulating since at least the Pliocene, based on information from fossil sister taxa outside the lake (Park and Downing, this volume). However, a pre-Pleistocene ostracod fossil record from Lake Tanganyika is currently unavailable, since no appropriate age outcrops of lake sediments occur surrounding the lake.

1. Composition of Ostracod Species Assemblages

Lake Tanganyika ostracods occur on a variety of substrate types, ranging from aquatic macrophytes to rocks on soft bottoms (sand and mud). A factor analysis comparison of endemic species occurring on soft-bottom substrates from 103 sampling localities (350 individuals counted per locality) around Lake Tanganyika shows that species are assorted into assemblages that broadly correspond to two major environmental variables (Figure 1). Factor 1 is closely related to substrate texture (sand versus mud), whereas factor 2 is mainly associated with the degree of sediment disturbance (high versus low sedimentation rates). Both of these variables are probably indirectly related to feeding behaviour (most species are non-selective detritus feeders) and to the ability of individual species to move on top of or interstitially within the sediment. However, when a factor analysis is performed on the similarity between site assemblages, rather than broad species’ habitat ranges, assemblages do not cluster along substrate (mud versus sand versus rock) habitat or by depth range, and no clear pattern is evident (Figure 2). Taken together, these data indicate that whereas individual ostracod species show
some habitat stenotopy, the species composition of any given assemblage is highly unpredictable.

2. Distribution of Ostracod Populations

Earlier studies have indicated that ostracod populations within Lake Tanganyika may be very patchy, with species being common in one location, yet rare or absent at a similar site, even within a distance of several hundred metres (Cohen, 1995). This patchiness exists even within areas that superficially appear to be of uniform habitat or substrate type. Most species have been found at only a very limited number of localities, as with many cichlid species from Lakes Malawi and Tanganyika (Brichtard, 1989; Ribbink et al., 1983). What is unusual about the distribution pattern of ostracods in Tanganyika (and sets them apart from most observations of cichlids) is the spatial distribution of rare taxa. Rare Malawi and Tanganyika cichlids tend to be clustered in geographically limited areas, often a single island or stretch of rocky coast, as regional endemics. In contrast, rare Tanganyika ostracods (ignoring species that have been found only at a single locality) are often widespread, with sampling localities separated by hundreds of kilometres, and few species qualify as regional endemics (Figure 3). This distribution pattern also supports the notion that geographical (and perhaps habitat) range limitations for these species are more a function of sampling bias against rare species than the actual distribution pattern of these taxa. Species assemblages
Fig. 2. Rotated factor analysis matrix for Tanganyika ostracod assemblages, by locality. R, rocky habitat; S, sandy habitat; M, muddy habitat. Note that locality assemblages do not cluster by either substrate type or depth.

can change so rapidly even within a habitat that cumulative $\alpha$ diversity (adding adjacent sites within a habitat type) can climb at least as quickly as cumulative $\beta$ diversity (between-habitat) curves (Figure 4a, b). Ongoing investigations are attempting to define the spatial scale over which this variability exists and the extent to which sampling resolution determines the pattern of patchiness that is inferred (S. Alin, unpubl.).

Fig. 3. Geographical range of Lake Tanganyika ostracod species. Distances are along the shoreline of the lake. Regional "endemics" are those species which have been found at multiple sites, all within 200 km (shoreline distance) of one another.
Fig. 4. Cumulative diversity with additional samples within and between habitats for Lake Tanganyika ostracods. (a) Along distance gradients (parallel to shoreline) within a given habitat (α diversity). Sample sites – Cape Banza, Luhanga and KM28.9 – were chosen as representative of low, intermediate and high disturbance regimes, respectively. (b) Along depth gradients between habitats (β diversity). As more samples are added, new species appear in the species pool. New species appear within habitats at approximately the same rate as they appear between habitats.
C. Models of Diversity Maintenance

Models of ancient lake community structure and integration have been strongly influenced by studies of both the morphology and feeding behaviour of cichlids. At an ecosystem level, and particularly for conservation planning purposes, it is important both to verify the hypotheses that have been derived from these studies, and to determine how relevant they are for other clades within ancient lake biotas.

The coexistence of numerous cichlid species with similar resource requirements has been used as evidence for the functionality of hyperspecialization in their pharyngeal jaw and tooth structure (Liem, 1978, 1980). However, this hypothesis has always been troubled by two facts. (i) Although cichlids show dietary differentiation, gut content analyses show that they consume a wide variety of food items, suggesting that these differences are facultative, not obligatory (e.g. Hori et al., 1993). (ii) Furthermore, the number of species that occurs within a given locality greatly exceeds the range of feeding guilds available. Nakai et al. (1994) have argued that these observations can be explained by retaining the hyperspecialization model by also invoking a behavioural component to the specialization (in one well-studied case, foraging behaviours that result in feeding mutualisms). However, the extent to which specific cichlid associations and feeding interactions observed at the primary LTER-type study site for this type of work (Mbemba) occur throughout the ranges of these species in Lake Tanganyika is unknown. Only by documenting the species associations and feeding interactions among these same cichlids at other localities around the lake might it be possible to determine whether they result from short-term contingencies of recruitment and locally learned behaviour, or are the result of coevolution dating to the divergence of the species involved in the association.

Even if feeding and behavioural specialization facilitate the coexistence and maintenance of high diversity in the Tanganyikan cichlids, this mechanism is unlikely to be useful in explaining the high diversity of ostracods in that lake. Tanganyikan ostracods show only modest habitat differentiation and substrate specificity, comparable to that seen in other non-diverse lacustrine faunas. Within-clade morphological specialization in Tanganyikan ostracod feeding and locomotory appendages is insignificant, and behavioural observations, although few, suggest that most species are non-selective detritus feeders. Body size differentiation (often implicated in feeding specialization) is also very limited within these clades.

Elsewhere the author has argued that the organization of the endemic ostracods into numerous metapopulations, rather than hyperspecialization, may be the mechanism for maintaining their high species diversity in Lake Tanganyika. This idea is supported by the frequent sympatry among numerous competitors whose resource requirements are remarkably similar (Cohen, 1994, 1995). Metapopulation dynamics as a mechanism for regenerating local,
ephemeral populations is consistent with the highly fragmented nature of the littoral and sublittoral habitats found in the lake, especially coupled with the poor dispersal capabilities of many endemic ostracod species. The relative importance of habitat fragmentation versus dispersal mode in structuring metapopulations would depend on the degree of substrate stenotopy shown by individual species. For species with strong habitat stenotopy (such as many cichlids and molluscs) degree of habitat fragmentation would be more important, whereas for habitat generalists (i.e. many ostracod species), rate of dispersal would be more important. Theoretically, if most species occur as transient populations in a habitat patch, then disequilibrium conditions may disallow the development of competitive dominance and higher local species diversity may result (Hanski, 1983). Under such circumstances local habitat patches may experience a continual flux of species, marked by local extinction and recolonization by a variety of species from adjacent populations.

D. Ostracod Palaeoecology

What do palaeoecological data reveal about the history of community stability and species diversity over longer time scales in Lake Tanganyika? Palaeoecological studies of lake-sediment cores of soft sand and mud substrates from relatively shallow water (40–70 m water depth) are now enabling analysis of community change at comparatively high temporal resolution and over much longer times intervals than ecologists can sample. Given average rates of sedimentation of 1–10 mm y⁻¹ at these water depths and bioturbation depths of c. 2–5 cm, one can expect a maximum sampling resolution of between 2 and 50 years (more typically 5–10 years), with sampling intervals measuring in the thousands of years.

Four cores were analysed in detail, chosen originally to represent a spectrum of physical disturbance regimes from river sedimentation. Core 86-DG-32 was collected near the Luamfi River delta in the southern, Tanzanian part of the lake. The Luamfi River watershed has a low human population (5–10 inhabitants km⁻²) and has experienced very little deforestation, and this core was selected to represent a low disturbance site. Core 86-DG-14 was collected offshore of the Dama River delta, central Burundi coast, in an area of intense, but not complete, deforestation, and represented an intermediate disturbance site. The remaining two cores, Bur-1 (Ruzizi River delta) and Karonge no. 3 (Karonge River delta), were collected from sites adjacent to heavily populated watersheds (c. 350 inhabitants km⁻²) that have experienced near total deforestation. These two cores represent sites of high physical disturbance. Details of these cores and their faunal lists are presented elsewhere (Wells et al., 1999).

Fossil ostracods present several advantages for detailed study over other taxa of benthic or epibenthic organisms commonly represented in the cores
(fish, insects, molluscs, sponges). They are abundant and diverse as fossils, generally well preserved and relatively easy to identify. For these reasons the following palaeoecological analyses and discussion will address only the ostracod fauna. The intention in carrying out these preliminary analyses of fossil ostracod fauna present in the core samples was to ask three questions. (i) What is the historical pattern of diversity difference between sites undergoing different disturbance regimes? (ii) Is an intensification of human disturbance recorded in these cores in the past few hundred years? (iii) How stable or unstable have ostracod species assemblages been over these time intervals?

The Karonge no. 3 core, collected 500 m offshore from the Karonge River delta, showed a clear increase in sedimentation rates over the past few decades and was almost barren of fossil invertebrates (Wells et al., 1999). As such, it was of little use in the present context and is not discussed further.

The other three cores all contained ostracod fossils, and within each core we analysed ostracod populations at approximately decadal resolution to understand patterns of community change and diversity. The data cover the last c. 1100 years, during which time independent data suggest that lake levels, water balance and major ion water chemistry have remained relatively stable (Cohen et al., 1997).

Cumulative and standing diversity plots for these three cores are shown in Figure 5. Core BUR-1 has by far the lowest standing diversity of the three sites, and standing diversity varies greatly between sampling horizons (x-axis). This difference is well evident before the rapid increase in population pressure and land degeneration of the twentieth century. If human activity is implicated in this difference, the threshold for having an effect on diversity must have been reached long before the twentieth century.

Standing diversities at intermediate and low disturbance site cores (86-DG014 and 86-DG-32, respectively) are much higher than the high-disturbance site (using a standardized sample size), as are all measured diversity indices (Fisher α, Shannon–Weiner and Simpson). Diversity in 86-DG-32 is relatively constant throughout the core. In 86-DG-14 diversity remains relatively constant except for one barren interval near the base of the core and a drop at the top of the core, which may be an anthropogenic signal.

Cumulative diversity curves display relatively rapid saturation of species (c. 50–100 years) for both the high and intermediate disturbance sites. In contrast, new species continue to appear at the low disturbance site throughout this c. 1100 year record. This continual appearance of new species despite a relatively constant standing species richness is indicative of a continual turnover of taxa. Significant species turnover and change is also indicated by the relatively low Jaccard similarity index values calculated for adjacent samples throughout the 86-DG-32 and 86-DG-14 cores (Wells et al., 1999). At the highly disturbed site (BUR-1) a pattern of co-ordinated local extinction and colonization is evident, with substantial faunal similarity between the species composition of stratigraphically adjacent samples.
Fig. 5. Cumulative and standing diversity curves of ostracods for cores taken at the three sites discussed in the text.

One explanation for the differences between these cores is that the low disturbance site contains the fossil record of numerous transient metapopulations which colonized the site over time. These species collectively contributed to maintain a high diversity, but individually were continually going extinct and recolonizing the site, without strong linkages to other sympatric species. Adjacent habitat patches both provided new colonists for the core site and were perhaps colonized by individuals from the study site. Conversely, at the more disturbed site, the interconnectedness of metapopulations may have broken down as a result of environmental perturbations becoming too severe. This would have led to fewer species being available to repopulate a locality. Such a scenario would explain the lower overall diversity at this site and, more importantly, why co-ordinated extinction and recolonization was the dominant pattern of faunal turnover. With a restructuring of community functions to allow competition to become important among a reduced but persistent pool of species, the integration of species interactions may have become tighter. A similar pattern of simultaneous local extinction and recolonization events has been observed in palaeolakes that have undergone major environmental fluctuations (salinity or lake level) during the Quaternary (e.g. Palacios-Fest et al., 1993; Magny et al., 1995).

Thus, the preliminary palaeoecological results are consistent with a view of considerable ecological change and an absence of species integration for ostracods over the 10–100 year time scale. However, this study is still in its infancy, and only through the study of many cores and other taxonomic groups
can generalizations be made about long-term ecological change in Lake Tanganyika. Exciting prospects for such understanding arise from ongoing efforts to obtain long cores (several hundreds of metres, spanning several million years of lake history) through scientific drilling in several of the African Great Lakes, including Tanganyika. Such cores promise to provide a view of the historical underpinnings of the ostracod radiation in Lake Tanganyika and its ecological dynamics.

IV. IMPLICATIONS FOR CONSERVATION BIOLOGY

It is now recognized that some areas of Lake Tanganyika are threatened by various human impacts. Threats from greatly increased rates of nearshore sedimentation caused by watershed deforestation and subsequent erosion are well documented (e.g. Cohen et al., 1993b), and there is a significant correlation between higher sedimentation rate and reduced diversity among ostracods, molluscs and fishes (Alin et al., 1999). A rapid increase in sedimentation is directly relevant to questions of habitat and population fragmentation because many benthic and epibenthic species of invertebrates and fish are sensitive to sediment loading, as it interferes with feeding and, particularly on rocky habitats, reduces habitat heterogeneity. As such, the extent to which extreme specialization and niche partitioning or continuous disequilibrium/metapopulation fragmentation regulate species diversity is of more than theoretical interest, and impinges upon habitat management and conservation decision making.

Based on the findings from these studies of ostracod assemblages, past and present, and those of cichlid fishes, several informed recommendations can be made. It is clear that reserve designs should incorporate an understanding of how permanent or ephemeral species are at the proposed reserve site, recognizing that stability may vary greatly among various components of the community. For example, if fish communities at a given locality are the sole target for preservation and they prove to be stable entities in Lake Tanganyika, with high persistence, then recruitment from adjacent habitat patches is a less important consideration in determining the area to be covered by a reserve. In such circumstances reserves that cover relatively small areas and that remain undisturbed might be viable. Conversely, conservation efforts might be directed more broadly to encompass both highly variable and stable elements of the biota. If recruitment from adjacent parts of numerous metapopulations is required for periodically rescuing habitat patches (sensu Brown and Kodric-Brown, 1977), then reserves must be designed to link adjacent habitat patches and should be larger. Elimination of adjacent patches (or the deterioration of their quality) could lead to a cascading sequence of extinctions, both directly, through a loss of recolonization potential, and indirectly, by eliminating the
very population structure that originally facilitated the high $\alpha$ diversity among competitors.

In the author's view, conservation and biodiversity management for Lake Tanganyika should take a broad, ecosystem-level approach, and avoid focusing only on high-visibility flagship taxa or on those with greatest immediate economic importance (Cohen, 1994). The contrast between cichlid and ostracod diversity structure in space and time suggests that no one taxonomic group is likely to serve as a robust model for how diversity is maintained or how ancient lake communities function as a whole. Only by combining palaeoecological and LTER data for multiple taxonomic groups are we likely to attain sufficient understanding of ecosystem change and species interactions over the 10–100 year time scale required for making informed decisions about conservation management practices in ancient lakes.

ACKNOWLEDGEMENTS

Research was funded by NOAA-NURC-UCAP grant no. UCAP-92-04, and NSF grants BSR 8415289, BSR 869074 and EAR 9627766. The author thanks the governments of Burundi, Tanzania and the Democratic Republic of Congo for providing numerous research permits for this work, as well as S. Alin, D. Dettman, K. Martens, E. Michel, C. O'Reilly, L. Park, T. Wells and K. West, all of whom continue to teach the author new things about Lake Tanganyika. This is publication no. 54 of IDEAL (the International Decade of East African Lakes).

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